Joint Nordic Test Day Model: Variance Components

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Abstract

This is one of the three papers describing the joint Nordic test day model for yield traits. Three Nordic evaluations will be presented: Red breeds, Holstein, and Jersey. The focus of this paper is on the definition of reduced rank random regression model describing the animal effects. Each country-breed submodel has its own variances and environmental correlations. Heritabilities and genetic correlations used in the models are illustrated.

1. Introduction

During the last decade Nordic countries have significantly increased the exchange of top semen across countries. Moreover, also test sires have been used across borders. It was recognized that the test resources would be more effectively used if the animal genetic evaluations of Finland, Sweden and Denmark could be joined. The development of the joint Nordic test day (TD) model started in 2002. Coordination of the project was done by Nordic Cattle Genetic Evaluation, a company jointly owned by breeding industries in these countries.

To speed up the development each country was allowed to have a national model that best suited to the local data. At the same time the model was expected to give unique ranking across Nordic countries. This was planned to be solved by first developing national models and then combining them into a *meta-model*.

Hereafter we will concentrate on the random animal effects of the model. The environmental effects are described in Lidauer *et al.* (2006) and the breeding value estimates are discussed in Pösö, *et al.* (2006).

2. Nordic Meta-models

In evaluations until 2006 Finland used a multiple trait TD model with first and later lactations as different traits. All lactations were used. Denmark used single trait and Sweden multitrait repeatability models for the first three lactation 305d records. In the joint model Finland and Denmark use TD data while Sweden still stays in the 305d lactation records.

The joint evaluations are run in three groups: Red breeds, Holstein and Jersey breed group. Because of small herd size and many mixed breed herds, Finland has evaluated all national breeds simultaneously. Therefore it was decided to include all Finnish cows in both the Red breeds and Holstein evaluations. Finland did not participate on Jersey run. In the final meta-model each country had their own sub-models with their own variances, but the genetic correlations across countries were forced to one.

2.1 Meta-model equation

Consider $\mathbf{y}^m$ to represent all observations in country *m,* multiplied by corresponding country-trait-herd-year heterogeneous variance adjustment factors (see, Lidauer *et al.,* 2006). The meta-model for random animal effects can be summarized by equation:

$$\begin{pmatrix}\mathbf{y}^{dk}\\ \mathbf{y}^{fi}\\ \mathbf{y}^{se}\end{pmatrix}=\begin{pmatrix}\boldsymbol{\beta}^{dk}\\ \boldsymbol{\beta}^{fi}\\ \boldsymbol{\beta}^{se}\end{pmatrix}+\begin{pmatrix}\mathbf{Z}_a^{dk}\\ \mathbf{Z}_a^{fi}\\ \mathbf{Z}_a^{se}\end{pmatrix}\mathbf{a}+$$
$$\begin{pmatrix}\mathbf{Z}_p^{dk} & 0 & 0\\ 0 & \mathbf{Z}_p^{fi} & 0\\ 0 & 0 & \mathbf{Z}_p^{se}\end{pmatrix}\begin{pmatrix}\mathbf{p}^{dk}\\ \mathbf{p}^{fi}\\ \mathbf{p}^{se}\end{pmatrix}+\begin{pmatrix}\mathbf{e}^{dk}\\ \mathbf{e}^{fi}\\ \mathbf{e}^{se}\end{pmatrix} \quad (1)$$

where $\boldsymbol{\beta}^{m}$, $\mathbf{Z}_a^m\mathbf{a}$, $\mathbf{Z}_p^m\mathbf{p}^m$, and $\mathbf{e}^m$ describe the environmental, breeding value (BV), non-genetic cow and measurement error effects for all traits in country *ma,* respectively. For Finland and Denmark the observations in $\mathbf{y}^{fi}$ and $\mathbf{y}^{dk}$ are TD observations, and for Sweden $\mathbf{y}^{se}$ are 305d observations.

2.2 Country models

For Denmark the three lactations and the traits milk, protein and fat were modeled using multi trait (MT) random regression model with second order polynomial appended, for trait j, with Wilmink term exp(-c_j*dim), where c_j was 0.05 for milk, and 0.04 for fat and protein, and dim the days in milk after calving. Within each lactation the rank of non-genetic cow, and within first lactation, the rank of BV functions, were reduced from total of 12 (i.e., three traits, 4 equations/trait) to 6, and for second and third lactation BV effects from 24 to 8.

Thus, the three lactation TD model applied to Danish data was written as:

$$\begin{pmatrix}\mathbf{y}^{dk}_{1i}\\ \mathbf{y}^{dk}_{2i}\\ \mathbf{y}^{dk}_{3i}\end{pmatrix}=\begin{pmatrix}\boldsymbol{\beta}^{dk}_{1i}\\ \boldsymbol{\beta}^{dk}_{2i}\\ \boldsymbol{\beta}^{dk}_{3i}\end{pmatrix}+\begin{pmatrix}\mathbf{Z}^{dk}_{a1i} & 0\\ 0 & \mathbf{Z}^{dk}_{a2i}\\ 0 & \mathbf{Z}^{dk}_{a3i}\end{pmatrix}\begin{pmatrix}\mathbf{a}_{1i}\\ \mathbf{a}_{23i}\end{pmatrix}+$$
$$\begin{pmatrix}\mathbf{Z}^{dk}_{p1i} & 0 & 0\\ 0 & \mathbf{Z}^{dk}_{p2i} & 0\\ 0 & 0 & \mathbf{Z}^{dk}_{p3i}\end{pmatrix}\begin{pmatrix}\mathbf{p}^{dk}_{1i}\\ \mathbf{p}^{dk}_{2i}\\ \mathbf{p}^{dk}_{3i}\end{pmatrix}+\begin{pmatrix}\mathbf{e}^{dk}_{1i}\\ \mathbf{e}^{dk}_{2i}\\ \mathbf{e}^{dk}_{3i}\end{pmatrix} \quad (2)$$

where $\mathbf{y}^{dk}_{ti}$ are the observations of milk, fat and protein production of the cow i for parity t, and $\mathbf{Z}^{dk}_{ati}$ and $\mathbf{Z}^{dk}_{pti}$ are covariable matrices of eigen functions for lactation t for BV and for non-genetic cow functions, respectively. For each lactation trait group the environmental effects $\boldsymbol{\beta}_t$ can be different. Each row in $\mathbf{Z}^{dk}_{ati}$ and $\mathbf{Z}^{dk}_{pti}$ depends on biological trait and dim of the observation, but the same random equations $\mathbf{a}_{ti}$ and $\mathbf{p}^{dk}_{ti}$ will associate with all biological traits in appropriate parity group.

Finnish model had the same structure except that lactations higher than three were included as repeated observations of third lactation traits. Here we present the model for a cow *i* with observations in four lactations, but the reader can extend the model for any number of later lactations:

$$\begin{pmatrix}\mathbf{y}^{fi}_{1i}\\ \mathbf{y}^{fi}_{2i}\\ \mathbf{y}^{fi}_{3i}\\ \mathbf{y}^{fi}_{4i}\end{pmatrix}=\begin{pmatrix}\boldsymbol{\beta}^{fi}_{1i}\\ \boldsymbol{\beta}^{fi}_{2i}\\ \boldsymbol{\beta}^{fi}_{3i}\\ \boldsymbol{\beta}^{fi}_{4i}\end{pmatrix}+\begin{pmatrix}\mathbf{Z}^{fi}_{a1i} & 0\\ 0 & \mathbf{Z}^{fi}_{a2i}\\ 0 & \mathbf{Z}^{fi}_{a3i}\\ 0 & \mathbf{Z}^{fi}_{a4i}\end{pmatrix}\begin{pmatrix}\mathbf{a}_{1i}\\ \mathbf{a}_{23i}\end{pmatrix}+$$
$$\begin{pmatrix}\mathbf{Z}^{fi}_{p1i} & 0 & 0 & 0 & 0\\ 0 & \mathbf{Z}^{fi}_{p2i} & 0 & 0 & 0\\ 0 & 0 & \mathbf{Z}^{fi}_{p3i} & \mathbf{Z}^{fi}_{p3i} & 0\\ 0 & 0 & \mathbf{Z}^{fi}_{p4i} & 0 & \mathbf{Z}^{fi}_{p4i}\end{pmatrix}\begin{pmatrix}\mathbf{p}^{fi}_{1i}\\ \mathbf{p}^{fi}_{2i}\\ \mathbf{p}^{fi}_{3i}\\ \mathbf{w}_{3i}\\ \mathbf{w}_{4i}\end{pmatrix}+\begin{pmatrix}\mathbf{e}^{fi}_{1i}\\ \mathbf{e}^{fi}_{2i}\\ \mathbf{e}^{fi}_{3i}\\ \mathbf{e}^{fi}_{4i}\end{pmatrix} \quad (3)$$

In (3), each lactation after 2nd are described by the same BV coefficients $\mathbf{a}_{23i}$, and by the same later lactation cow wise non-genetic coefficients $\mathbf{p}^{fi}_{3i}$. The eigen function covariables in $\mathbf{Z}^{fi}_{a3i}$ and $\mathbf{Z}^{fi}_{p3i}$ dependent on dim and biological trait of particular observation. In addition, each lactation model after the second have unique within lactation non-genetic cow effects $\mathbf{w}_{3j}$. For any lactation after third, say 3^+, the covariables $\mathbf{Z}^{fi}_{a3+i}$ and $\mathbf{Z}^{fi}_{p3+i}$ for the same dim and biological trait are the same as for third lactation.

The Swedish model for 305d observations was derived from the Danish model (2) as described in Mäntysaari (2002). First, the 305d observations were assumed to result from a sum of ten TD observations on standard dims, i.e. 15,45,…,285. Accordingly, the corresponding rows of eigen function covariables in (2) were summed up to form rows $\mathbf{z}^{305}_{\bullet t}$ for new design matrices:

$$\begin{pmatrix} y_{1i}^{305} \\ y_{2i}^{305} \\ y_{3i}^{305} \end{pmatrix} = \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix} + \begin{pmatrix} \mathbf{z}_{a1}^{305} & 0 \\ 0 & \mathbf{z}_{a2}^{305} \\ 0 & \mathbf{z}_{a3}^{305} \end{pmatrix} \begin{pmatrix} \mathbf{a}_{1i} \\ \mathbf{a}_{23i} \end{pmatrix} + \begin{pmatrix} \mathbf{z}_{p1}^{305} & 0 & 0 \\ 0 & \mathbf{z}_{p2}^{305} & 0 \\ 0 & 0 & \mathbf{z}_{p3}^{305} \end{pmatrix} \begin{pmatrix} \mathbf{p}_{1i} \\ \mathbf{p}_{2i} \\ \mathbf{p}_{3i} \end{pmatrix} + \begin{pmatrix} e_{1i}^{305} \\ e_{2i}^{305} \\ e_{3i}^{305} \end{pmatrix} \quad (4a)$$

Since in (41) the sub-model for non-genetic cow effects has 6 coefficients in each lactation, the terms were summed to give only one permanent environment effect per lactation and trait:

$$\begin{pmatrix} y_{1i}^{305} \\ y_{2i}^{305} \\ y_{3i}^{305} \end{pmatrix} = \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix} + \begin{pmatrix} \mathbf{z}_{a1i}^{305} & 0 \\ 0 & \mathbf{z}_{a2i}^{305} \\ 0 & \mathbf{z}_{a3i}^{305} \end{pmatrix} \begin{pmatrix} \mathbf{a}_{1i} \\ \mathbf{a}_{23i} \end{pmatrix} + \begin{pmatrix} p_{1i}^{305} \\ p_{2i}^{305} \\ p_{3i}^{305} \end{pmatrix} + \begin{pmatrix} e_{1i}^{305} \\ e_{2i}^{305} \\ e_{3i}^{305} \end{pmatrix} \quad (4b)$$

Each 305d trait is recorded only once per lactation, and the model is still over-parameterized. However, the permanent environment effects were kept in model to make the measurement error variance matrices block diagonal as was already in models (2) and (3). This gave computational efficiency because of more flexible data structure.

2.3 Variance parameters

In the models (2), (3) and (4b) the variances for permanent environment ($\mathbf{p}^m_{ti}$) and for measurement errors ($\mathbf{e}^m_{ti}$) were defined within country. As the BV function coefficients ($\mathbf{a}_{ti}$) are the same in all countries each animal has only one set of BVs. However, within each country the covariables in $\mathbf{Z}^m_{ati}$ are different. This leads to different expression of the BV function $\mathbf{Z}^m_{ati}\mathbf{a}_{ti}$ in each country, and thus different daily genetic variances.

The variances were derived by fitting covariance functions (CF) into MT genetic and residual (co)variance matrices $\mathbf{G}_0$ and $\mathbf{R}_0$ estimated for all traits in three lactations and five lactation stages. The CF derivation and rank reduction was done as in Koivula *et al.* (2004), extended for MT TD model in Mäntysaari (2006).

The way to divide the Finnish non-genetic third lactation variation $\text{var}(\mathbf{Z}_{3i}\mathbf{p}_3 + \mathbf{e}_3)$ into $\text{var}(\mathbf{Z}^{fi}_{3i}\mathbf{p}^{fi}_t + \mathbf{Z}^{fi}_{p3i}\mathbf{w}_t + \mathbf{e}^{fi}_t)$ in (3) depends on repeatability of the traits. For this the phenotypic correlations of traits between the second and the third lactation were used. Emmerling *et al*., (2002) suggested a simple concept for a single trait RR, but for multiple biological traits one needs to account for the differences of phenotypic correlations within lactation and across lactations. The method applied here is described in Mäntysaari (2006).

The MT variance component estimation was done for Finnish Ayrshire (FAY) (J. Pösö, 2002; unpublished), for Danish Holstein, Red Dane (RDM) and Jersey (Jacobsen *et al.,* 2002). The genetic correlations between biological traits, lactation stages, and across lactations, specified by breed wise $\mathbf{G}_0$ were averaged over breeds in Red breed meta-model, i.e., the genetic correlations were average of FAY and RDM. The unified model for 305d yields was first constructed for RDM (and Holstein), and thereafter modified for Swedish Red (and Swedish Holstein). In the modification the covariables in $\mathbf{z}^{dk}_{ati}$ were scaled appropriately $\mathbf{z}^{305}_{at} = \tau_t \mathbf{z}^{dk}_{at}$, to attain heritabilities estimated for Swedish 305 d production (E. Carlen and E. Strandberg, 2005; unpublished).

3. Heritabilities and genetic correlations

Figure 1 shows the daily heritabilities for three lactations in Holsteins and for FAY. In the Red breed evaluation, the shape of heritability curves for RDM (not given here) were similar to Holstein. Notable differences that exist in daily heritabilities become less when the RR model is used to derive heritabilities for the "standard ten test day" 305d yields. Table 1 lists 305d heritabilities for all traits and breeds in three Nordic evaluations. In Holstein and in Red breed evaluations records of both Finnish breeds are modeled using the parameters derived for Finnish "all lactations" repeatability model. Thus, in Holstein evaluation the heritabilities for the first three lactations for all

Finnish cows were as for Holstein in Table 1 and in Red breeds run, all Finnish cows were modeled using the parameters given for Ayrshire (Table 1).

Genetic correlations among traits and 305d lactations for Holsteins are given in Table 2 and for Red breeds in Table 3. For Jersey, see Mäntysaari *et al.* (2006). The phenotypic correlations between traits are breed depended, and the ones given in Table 3 are for FAY. In Table 3 the later lactation parameters are illustrated by giving correlations among first four lactations. Any lactation after three would have had the same parameters as the third.

4. Summary on NAV model

The *meta-model* for Nordic evaluations allows i) to combine TD records and lactation records; ii) to define different genetic variances, different heritabilities and different repeatabilities and phenotypic correlations in each country but still constrains the genetic correlations to be the same in each country and unity across countries; iii) some of the traits to have repeated observations. As the environmental submodels of the breeds are different, it is also justified to assume different heritabilities in different countries. This assures proper accounting of differences in information (number of TDs, number of daughters etc.). However, different heritabilities can also lead into differences in variation of BV estimates in different countries. In Nordic joint evaluation this was adjusted in a heterogeneous variance adjustment process (Lidauer *et al.,* 2006).

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Table 1. Heritabilities of 305d milk, protein and fat for each parity for each breed in Nordic test day evaluations. For Finnish and Danish breeds the values are derived from test day model.

Trait /lactation	Jersey	Red breeds			Holstein	
		Red Dane RDM	Finnish Ayr-shire FAY	Swedish Red SRB	Danish Finnish test day	Swedish
Milk 1	0.44	0.41	0.38	0.38	0.33	0.43
Protein 1	0.38	0.35	0.26	0.36	0.31	0.35
Fat 1	0.35	0.41	0.27	0.37	0.33	0.36
Milk 2	0.47	0.24	0.30	0.27	0.28	0.29
Protein 2	0.23	0.21	0.23	0.30	0.28	0.25
Fat 2	0.22	0.28	0.27	0.31	0.35	0.29
Milk 3	0.27	0.20	0.30	0.22	0.29	0.27
Protein 3	0.23	0.19	0.23	0.27	0.28	0.25
Fat 3	0.23	0.25	0.24	0.26	0.35	0.29

Table 2. Genetic (above diagonal) and phenotypic correlations (below diagonal) for 305d yield derivatives in Holstein breed group.

	Lactation 1			Lactation 2			Lactation 3		
	Milk	Prot	Fat	Milk	Prot	Fat	Milk	Prot	Fat
Milk 1		0.86	0.46	0.85	0.71	0.23	0.81	0.63	0.09
Prot 1	0.93		0.67	0.75	0.85	0.46	0.71	0.81	0.33
Fat 1	0.77	0.85		0.42	0.68	0.85	0.43	0.70	0.78
Milk 2	0.48	0.45	0.36		0.84	0.42	0.99	0.78	0.32
Prot 2	0.44	0.48	0.43	0.95		0.72	0.84	0.99	0.62
Fat 2	0.32	0.39	0.49	0.82	0.89		0.47	0.76	0.98
Milk 3	0.43	0.41	0.33	0.43	0.41	0.33		0.79	0.37
Prot 3	0.39	0.43	0.40	0.39	0.44	0.39	0.94		0.69
Fat 3	0.24	0.31	0.42	0.30	0.37	0.44	0.83	0.88	

Table 3. Genetic (above diagonal) for 305d yield derivatives in Red breeds *meta-model* and phenotypic correlations (below diagonal) for Finnish Ayrshire.

	Lactation 1			Lactation 2			Lactation 3			Lactation 4		
	Milk	Prot	Fat	Milk	Prot	Fat	Milk	Prot	Fat	Milk	Prot	Fat
Milk 1		0.86	0.46	0.85	0.71	0.23	0.81	0.63	0.10	0.81	0.63	0.10
Prot 1	0.92		0.68	0.75	0.85	0.47	0.71	0.81	0.33	0.71	0.81	0.33
Fat 1	0.69	0.79		0.42	0.68	0.84	0.43	0.70	0.78	0.43	0.70	0.78
Milk 2	0.71	0.68	0.49		0.84	0.43	0.99	0.78	0.32	0.99	0.78	0.32
Prot 2	0.65	0.70	0.58	0.91		0.72	0.84	0.99	0.63	0.84	0.99	0.63
Fat 2	0.42	0.52	0.65	0.63	0.75		0.47	0.77	0.98	0.47	0.77	0.98
Milk 3	0.61	0.58	0.43	0.56	0.48	0.32		0.79	0.38	1.00	0.79	0.38
Prot 3	0.54	0.59	0.52	0.47	0.51	0.41	0.88		0.69	0.79	1.00	0.69
Fat 3	0.31	0.41	0.56	0.28	0.37	0.50	0.62	0.76		0.38	0.69	1.00
Milk 4	0.61	0.58	0.43	0.56	0.48	0.32	0.55	0.47	0.30		0.79	0.38
Prot 4	0.54	0.59	0.52	0.47	0.51	0.41	0.47	0.50	0.38	0.88		0.69
Fat 4	0.31	0.41	0.56	0.28	0.37	0.50	0.30	0.38	0.47	0.62	0.76	

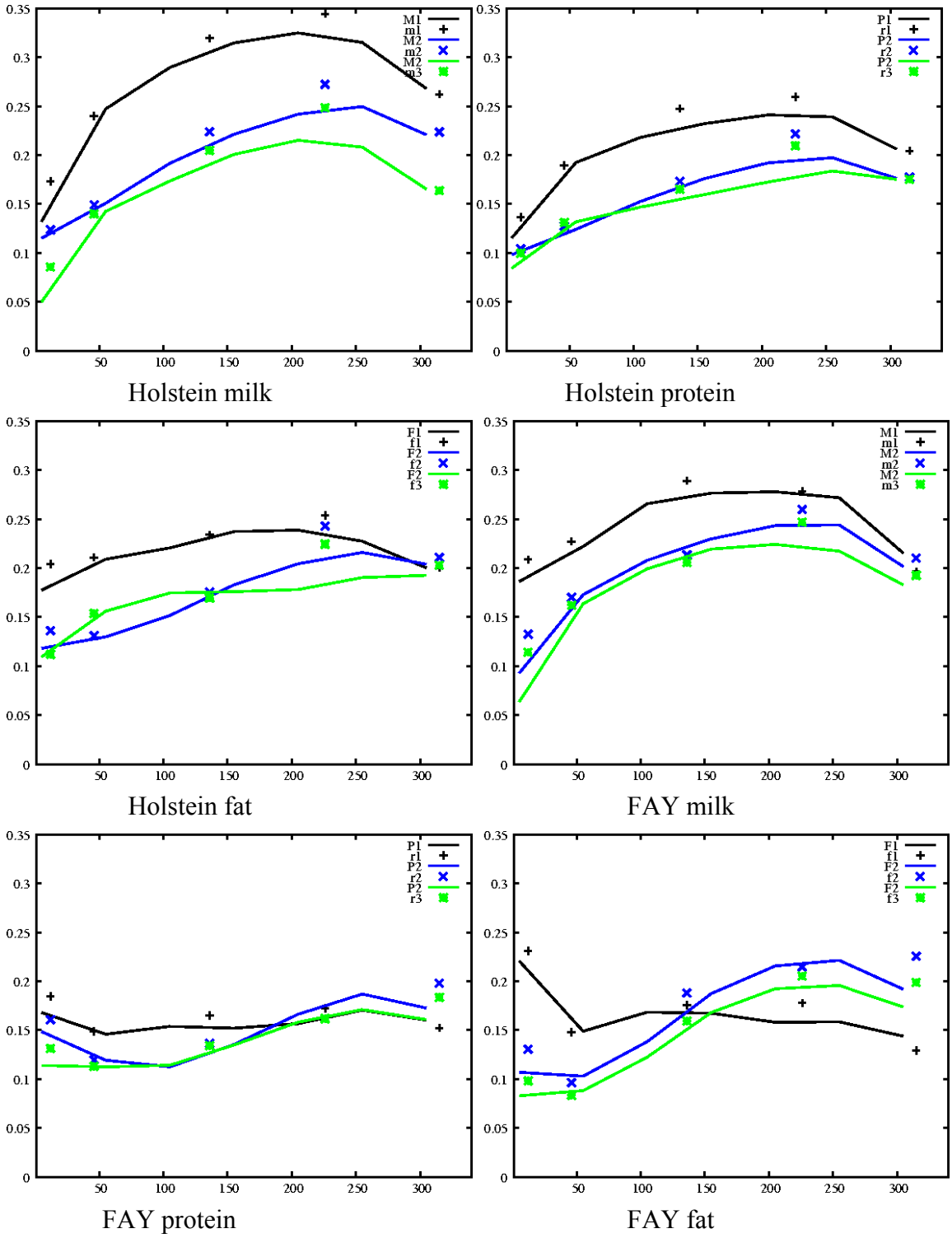

Figure 1. Daily heritabilities for milk, protein and fat on Holstein evaluation and on Finnish Ayrshire (FAY) Red breeds evaluation. The lines display the values in use in joint evaluation for each lactation, and the markers display the heritabilities estimated by multitrait variance components analyses.